NOTES ON THE NERVOUS SYSTEM OF THE PELECYPODA.

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Read 11th December, 1903.

In *Nature*[1] for October 29th is a letter from Mr. Latter, of Charterhouse School, in which attention is called to the presence in an individual specimen of *Anodonta* of a ganglionic enlargement situated on the left cerebro-visceral connective in front of the pericardium. Such abnormal ganglia have apparently been noted before, and are of considerable interest in so far as they assist in the determination of the homologies of the different masses of ganglionic matter that compose the central nervous system of the Pelecypods.

In the case before us Mr. Latter, taking for granted the soundness of the generally accepted view that in the cerebro-visceral system of Pelecypods are to be found representatives of the cerebral and pleural ganglia of the Gastropod in a degenerate condition, speaks of this ganglion as the "pleural," and infers therefore that the Pelecypod cerebral ganglion is cerebral pure and simple, strictly comparable to the cerebral ganglion of the Gastropod, and not, as is now most frequently taught, a fusion of originally separate cerebral and pleural ganglia.

Assuming that any direct comparison between the individual nerve centres of the cerebro-visceral system of Pelecypods and Gastropods is justifiable, there seems little reason to criticise Mr. Latter's interpretation of this abnormal ganglion, but as, for my part, I very much doubt whether we have any right to such an assumption, I am glad to take this opportunity to emphasise views lately put forward on this subject by Dr. Gilman Drew,[2] and to add some details in corroboration of such views.

The point of view, the objections to which I wish to urge, was propounded by Pelseneer, and so far as concerns the Pelecypods is briefly stated in the *Comptes Rendus* for 1890,[3] and at greater length in the Archives de Biol. for the following year.[4] In these papers he points to the presence in certain members of the Protobranchs of two serially disposed ganglia in place of the simple cerebral ganglion normal to the Pelecypoda, and also to separate connectives passing from these two enlargements to the pedal ganglia, as evidence of the possession by the Pelecypod stock of a nervous system of the Gastropod type, characterised by independent cerebral and pleural ganglia each united by a connective to the pedal ganglia.

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[1] *Nature*, vol. lxviii (1903), p. 623.

[2] Drew, "The Life-History of *Nucula delphinodonta*": Quart. Journ. Micro. Sci., vol. xliv (1901), p. 372.

[3] Pelseneer, "Sur l'identité de composition du système nerveux central des Pélécypodes et des autres Mollusques": C.R. Ac. Sci., t. cxi, p. 245.

[4] Pelseneer, "Contribution à l'étude des Lamellibranches": Arch. Biol., t. xi.

On the other hand, Drew, in dealing with the central nervous system of *Nucula delphinodonta*,[1] strongly insists upon its essentially primitive nature, and finds neither in the developmental processes through which it passes nor in the adult condition any sure indication of the Gastropod type of specialisation. Apart from the generalised structure of the nervous system as a whole, his two main points are — (1) that the cerebral ganglia develop from a single rudiment on either side, without signs of a pleural enlargement, and (2) that there is no indication of a pleural enlargement in the adult either of this species of *Nucula* or in the other forms of Protobranchiata examined by him. Another fact of some importance in connection with his general conclusions is furnished by the mode of development of the cerebro-visceral connectives. He writes:[2] "They are first found very close to the surface, almost, if not quite, in contact with the ectoderm. Later they sink deeper into the body. The cerebro-visceral commissures are quite thick, and differ from the cerebro-pedal commissures in having much the same structure as the ganglia themselves."

It will be remembered that Pelseneer's comparison was suggested not only by the double cerebral ganglia found by him and Stempell[3] in several Protobranchs, but also by the corresponding duplicity of the cerebro-pedal connectives. This duplicity of the connectives has been confirmed by Drew, but he suggests that possibly the posterior of the two roots—the pleuro-pedal connective according to Pelseneer and Stempell—is the proximal end of the otocystic nerve, and not really a connective at all. In Pelecypods the otocystic nerve arises in the cerebral ganglion, and normally accompanies the cerebro-pedal connective, intimately blended with it, to a point near the pedal ganglion, and then branches off to the otocyst. In *Solenomya*, however,[4] the nerve has been found to leave the cerebral ganglion independently behind the pedal connective, and to run entirely free to the otocyst. This fact suggested to Drew that possibly in the Protobranchs with two roots to the cerebro-pedal connectives, a transitional stage between *Solenomya* and the normal condition is realised, in which the proximal and distal ends of the otocystic nerves are free, while the intermediate parts are fused with the cerebro-pedal connectives. This idea is strengthened by the fact that the distal, free part of the otocystic nerve in *Nucula* is of the same calibre as the posterior root of the cerebro-pedal connective. The only objection, and a very important one, is that in *Solenomya* each pedal connective, although emerging single from the cerebral ganglion, arises within the ganglion by two independent roots. This is a point that requires further confirmation, but if confirmed it would be fatal to Drew's suggestion.

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[1] Drew, l.c., p. 370.

[2] Drew, l.c., p. 372.

[3] Stempell, "Beiträge zur Kenntniss der Nuculiden": Zool. Jahrb. (Fauna Chilensis), i (1898), p. 403.

[4] Stempell, "Zur Anatomie von *Solemya togata*": Zool. Jahrb., Bd. xiii (1899), p. 147.

In summing up, Drew concludes, in general terms, that[1] "it seems more likely that the nervous systems of all molluscs have been derived from some such generalised a type as found in *Chiton*, and that each class has developed ganglia according to its needs, than that the ancestors of the Lamellibranchs possessed the comparatively complex system of ganglia found in Gastropods."

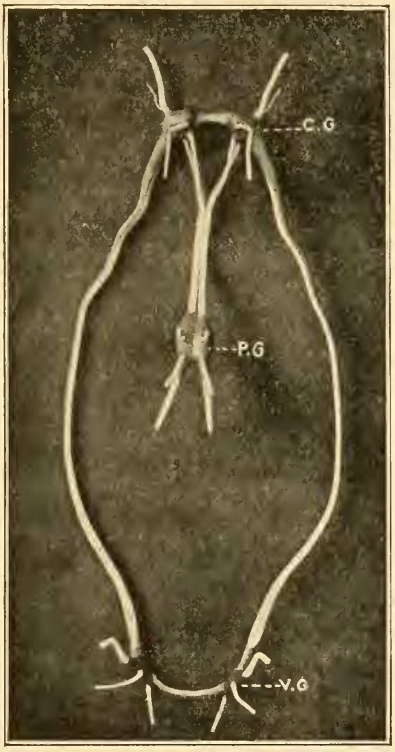

FIG. I.—Model of nervous system of *Nucula nucleus*, seen from the ventral aspect. C.G. cerebral ganglion; P.G. pedal ganglion; V.G. visceral ganglion.

During the last few years I have examined minutely several specimens of *Nucula nucleus*, and amongst other things have made a careful study of the nervous system by means of transverse and horizontal sections and by reconstruction after the Born (or rather Newton[2]) method. Upon the general conformation of this nervous

[1] Drew, l.c., p. 373.
[2] Newton, "On the Brain of the Cockroach": Quart. Journ. Micro. Sci., vol. xix (1879), p. 341.

system I need not dwell; it agrees in essentials with previous descriptions (Fig. I), but there are several points to which I must more particularly call attention. (1) There is no sign of any separation of the cerebral ganglion into cerebral and pleural enlargements. This point was shown in the first place in a model reconstructed from sections taken transversely to the long axis of the animal, and was confirmed by horizontal sections (Fig. II). (2) The cerebral ganglion has no definite posterior limit, but gradually tapers away (as described by Drew) into the cerebro-visceral connective, while the whole of this connective, or, in fact, the entire ring formed by the cerebral and visceral ganglia with their commissures and connectives, is to some extent ganglionic throughout. (3) The two roots of each cerebro-pedal connective rise from the inner side of the

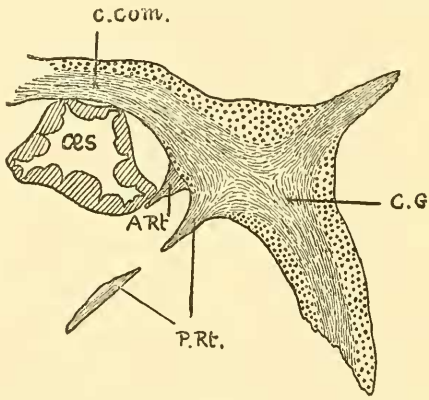

Fig. II.—Horizontal section of right cerebral ganglion of *Nucula nucleus*. A.RT. anterior root of cerebro-visceral connective; P.RT. its posterior root; C.COM. cerebral commissure; C.G. cerebral ganglion; ŒS. œsophagus.

cerebral ganglion, close together and both at a point posterior to the origin of the anterior pallial nerve, which according to Pelseneer should spring from the pleural enlargement. (4) The distal free part of the otocystic nerve is of practically the same diameter as the hinder root of the cerebro-pedal connective (as stated by Drew). (5) The pedal ganglia are united by two serially arranged commissures (Fig. III): a multiple connection between these ganglia, suggestive of the ladder-like condition in Amphineura and low Gastropods, has been noted by Rawitz in *Unio*,[1] and by Stempell[2] in certain Protobranchs, but has not hitherto been recorded for *Nucula*.

In conclusion, a few words with regard to Drew's comparison between the nervous systems of *Nucula* and an Amphineuran. In the Chitons (the most generalised Amphineura so far as concerns the nervous

[1] Rawitz, "Das zentrale Nervensystem der Acephalen": Jena Zeits., Bd. xx (1887), p. 438.
[2] Stempell: Zool. Jahrb. (Fauna Chilensis), i, p. 405.

system) the central nervous system, ignoring the parts concerned in the innervation of the buccal mass, consists essentially of an elongated loop (the cerebro-pallio-visceral loop) that encircles the body in a position just above the branchial furrow, and innervates the head, mantle, gills and viscera, and of two pedal cords in the foot, connected in front with the cerebral portion of this loop, and united irregularly by commissures. The cerebro-pallio-visceral loop has the same structure and similar relations to the body (except for its union posteriorly *above* and not below the gut) as the loop in *Nucula* formed by the cerebral and visceral ganglia with their commissures and the cerebro-visceral connectives. Both are ganglionic

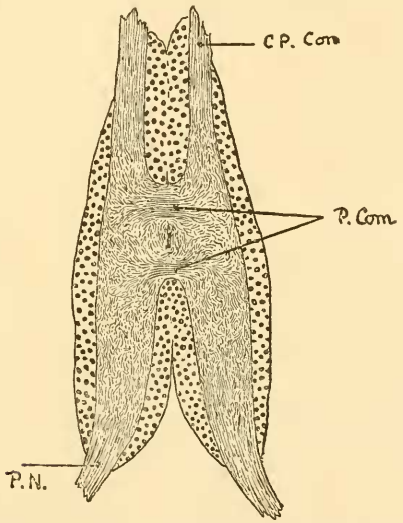

FIG. III.—Longitudinal section of the pedal ganglia of *Nucula nucleus*. C.P.CON. cerebro-pedal connective; P.COM. pedal commissures; P.N. pedal nerve.

throughout, both have the same position, and both innervate the same organs and regions of the body. In fact, they are without question homologous structures. The differences that do exist show that the loop in *Nucula* is somewhat specialised — the ganglionic matter is concentrated principally towards the anterior and posterior regions of the loop, forming definite though not sharply limited cerebral and visceral ganglia. These develop independently of the rest of the loop, although their connectives by their mode of development and adult structure show clearly enough that they once formed part of a continuous loop of ganglionic matter, now in process of replacement by connective fibres. The anterior and posterior concentration of ganglionic matter in this portion of the nervous system of Pelecypods is doubtless correlated to some extent with the special localisation of organs, characteristic of the class — as, for instance, the adductor muscles (derivatives of the pallial musculature), one at either end of

the body, the highly developed labial palps at the anterior end, the gills at the posterior end, and also, even probably to some extent in primitive forms, the extra sensitiveness of the hinder part of the mantle border.

The pedal ganglia show a higher grade of specialisation, even in the lowest types of Pelecypods, than in either Amphineura or low Prosobranchs. In the latter cases the ladder-like form, consisting of two longitudinal cords of ganglionic matter united at intervals by commissures, persists, and is no doubt intimately associated with a long creeping sole. In the Pelecypods, one of whose most striking characters is the adaptation of the general body form for digging, the foot has already been specialised as a digging organ even in the most primitive forms. For this purpose it has assumed a more or less cylindrical shape, with greatly restricted sole area. Corresponding to this change of form, the long pedal cords, which we may assume were present in ancestral forms, became shortened up to form rounded ganglia in which occasionally traces of the original ladder-like formation may be found in multiple commissures.

There is no doubt that the double cerebro pedal connectives found in several of the Protobranchia, unless their posterior roots prove to be the otocystic nerves, constitute a difficulty when comparing the Pelecypod nervous system with one of the Amphineuran type. Were it not for the occurrence of both otocystic nerve and double (though intra-ganglionic) roots to the cerebro-pedal connectives in *Solenomya*, there would be no question in my mind that Drew's interpretation of the posterior root of the cerebro-pedal connective as the otocystic nerve is correct. But in case further investigation of *Solenomya* should prove his view to be untenable, I venture to put forward the following suggestion:—May not the posterior root be the vestige of Amphineuran latero-pedal connectives? These connectives between the pallio-visceral loop and the pedal cords, it will be remembered,[1] reach their greatest and most characteristic development in the most generalised types of Polyplacophora (*Hanleya*, *Lepidopleurus*), but as specialisation increases they first become very variable both in position and number, and finally in the higher forms (*Tonicia*, *Ischnochiton*, *Acanthochiton*) vanish. As these connectives are characteristic of the lowest known form of molluscan nervous system, it is no great stretch of imagination to suppose that they also occurred in the forerunners of the Pelecypods, and in this group, as in the Chitons, vanished in proportion to the increase in general specialisation, until at the present day their remains persist in some few Protobranchs as a posterior root to the cerebro-pedal connective. In the light of this suggestion, it is interesting to recall that connections occasionally occur in Pelecypods between the visceral and pedal ganglia.[2]

Whether some such comparison as this, with a nervous system of the present-day Amphineuran type, is justified or not by the facts to

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[1] Plate, Zool. Jahrb. (Fauna Chilensis), Bd. ii (1902), p. 493.

[2] D'Hardvillier, "Sur quelques faits qui permittent . . . " : C.R. Ac. Sci., t. cxvii (1893), p. 250.

be observed in the most generalised living Pelecypods, I think there can be no doubt that the early progenitors of the Pelecypods and Gastropods were already distinct before there was any question of specialised ganglia in the cerebro-visceral part of the nervous system. This can be inferred from the occurrence at the present time, in each of these groups, of genera (e.g. *Pleurotomaria, Nucula*) in which this part of the nervous system shows only the very slightest indication of specialisation into individual ganglia.[1] Now each of these forms is far more specialised and typical of its class than its ancestors could have been when first they diverged from the common molluscan stock. So that it is legitimate to assume that at that time the cerebro-visceral system was an entirely unspecialised ganglionic loop.

Thus the facts at our disposal, and the inferences to be justly drawn from them, seem strongly to favour Drew's general conclusion, that the nervous systems of Gastropods and Pelecypods have arisen in a common generalised form, probably of the Amphineuran type, and that each class has developed ganglia independently, according to its needs.

To return finally to Mr. Latter's letter. It is clear that according to Drew's views set forth above, ganglia appearing sporadically upon the visceral connectives would have no direct homology to any particular ganglion of normal occurrence in this or any other group of molluscs, but would be a local retention of the ganglionic condition once common to the whole cerebro-visceral system, and are thus a reversion, not to a more specialised, but to a more generalised condition.

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[1] These nervous systems certainly do not represent the degenerate condition of a once more specialised type. Degeneration from a state with specialised and separate ganglia could hardly result in the formation of continuously ganglionic cords. Such are a sure sign of primitive generalisation.